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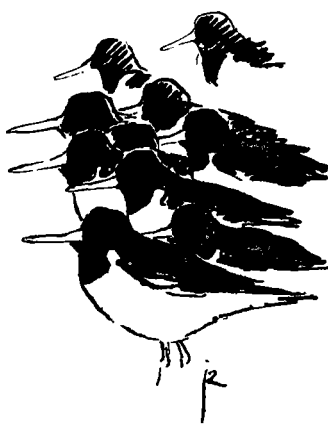
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WEIGHT LOSS IN OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS* ON THE ROOST AND AFTER CAPTURE

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Zwarts L., J.B. Hulscher & P.M. Zegers 1996. Weight loss in Oystercatchers *Haematopus ostralegus* on the roost and after capture. *Ardea* 84A: 13-20.



This paper analyses the weight loss in Oystercatchers on the roost and after capture and attempts to investigate to what degree this weight loss is due to defecation of digested food, to dehydration and to utilisation of nutrient stores. The study emphasizes the need to record weight changes relative to the time of arrival at the roost, rather than relative to time since capture, as is common practice in correcting for weight loss in captive birds. If food is still defecated, the weight loss is 4.3 times as large as when the gut is empty. From then on, probably 10% of the weight loss is due to dehydration. It is estimated that the rest of the remaining weight decrease is about equally due to loss of dry lean muscles and fat. The weight loss of waders of different size is a function of body weight^{3/4}.

Key words: Oystercatcher - *Haematopus ostralegus* - weight correction - dehydration - defecation

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INTRODUCTION

The body weight of individual birds varies during the day. A part of this variation has nothing to do with the change of the body weight itself, but with the variable amount of food stored in the alimentary tract. Oystercatchers *Haematopus ostralegus* arriving at the high water roost may contain up to 85 gram fresh food, which is equivalent to about 15% of the body weight (Dare & Mercer 1973). Body weight decreases after a feeding period has ended because digestion continues and undigested material is excreted (Kersten & Visser 1996a). When the gut is empty, weight loss continues, although at a lower rate, through catabolisation of the body reserves, as reviewed by Davidson (1983).

Waders are usually captured at high water roosts by cannon or mist netting. However, the number of birds caught in one catch and the time of capture relative to the time of arrival at the

roost differ markedly between occasions. Since the body weight decreases during the roosting period, a correction is needed to prevent the first weighed birds of a large catch being heavier, on average, than those weighed last. Thus average body weight always appears to be lower when more birds are caught, due to the increase in processing time (Wilson & Davidson 1982). This prompted us to measure the rate of weight loss in Oystercatchers throughout the roosting period in order to standardize the measured body weights to the time when Oystercatchers have emptied their gut and have not yet begun to utilize their nutrient stores.

METHODS

Oystercatchers were captured at high water roosts with cannon or mist nets. After capture, birds were kept outdoors in groups of 3-10 individuals

in perforated plastic crates or roofed cotton cages. The data were from Zwarts *et al.* (1996a), where a description of the study area and an account of the morphometric measurements, determination of the body composition and the statistical analyses can be found. The weight correction for variation in body size has been described elsewhere (Zwarts *et al.* 1996c).

In order to correct in a standard way for weight loss due to digestion, it is necessary to know the time at which the captured birds stopped feeding. Oystercatchers feeding on the tidal flats in our study area arrive at the high water roost when the water level is 20 cm above mean sea level, so we expressed all the capture and weighing times relative to the time at which the incoming water table reached this level. The immersion times were taken from continuous records of the water level at the nearby station of Rijkswaterstaat at Lauwersoog.

Weight loss was analysed in three ways. First, 364 birds were weighed twice at intervals varying in most cases between 1 and 13, but exceptionally 48, hours. Birds were weighed only twice to reduce stress and thus, possibly, extra weight loss (Davidson 1983). Second, we selected 2615 Oys-

tercatchers that had been captured on 33 days during which so many birds were caught in one catch that the last bird was weighed at least three hours after the first. We calculated for each of these days the average weight of the birds at each hour after capture. Since the average body weight varied between days, we expressed for each day the weight at each hour as a deviation from the average weight four hours after arrival at the roost. Third, the water contents of 90 casualties, usually birds with leg cramp, were related to the time since their arrival at the roost. We determined in these birds the fresh weight at death, and later on in the laboratory, where they were stored in a freezer, the dry weight and, by subtraction, the amount of body water. In the same sample of birds, we also measured fat and dry lean weight (see Zwarts *et al.* 1996a).

RESULTS

The majority of the Oystercatchers were netted during the incoming tide. Some were captured immediately after their arrival at the high water roost, while others were caught after they had roosted for up to seven hours. The initial rate of weight loss in birds captured on arrival at the roost was high, but the rate declined in birds caught hours later (Fig. 1). Birds lose on average 8 g h^{-1} between two weighings when the first weighing was made within one hour of their arrival at the roost. But when the roosting period preceding the first weighing exceeded two hours, Oystercatchers lose less than 3 g h^{-1} (Fig. 1). In birds weighed at, or just, after arrival at the roost, the weight loss per hour decreased with the length of the interval between the first and second weighings (Fig. 2, upper line), a trend that was absent in birds first caught more than two hours into the roosting period (Fig. 2, lower line). Clearly, weight change must be described by plotting weight loss relative to the end of the feeding period rather than to the length of time the birds has been held in captivity.

It is clear from Figs. 1 & 2 that the initial

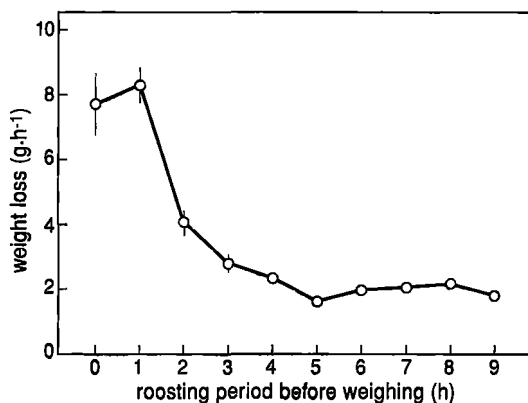


Fig. 1. Loss of body weight ($\text{g h}^{-1} \pm \text{SE}$) between two weighings in individual Oystercatchers ($n = 364$) in relation to the length of the preceding roosting period, i.e. the period between the arrival at the roost and the time of the first weighing.

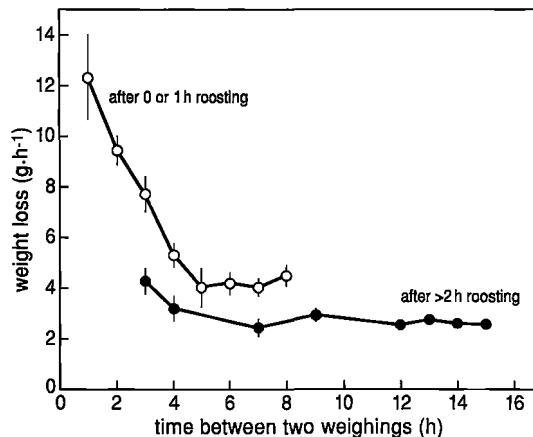


Fig. 2. Loss of body weight ($\text{g h}^{-1} \pm \text{SE}$) between two weighings in individual Oystercatchers in relation to the duration of the interval between two weighings, given separately for birds in which the first weighing took place within one hour of their arrival at the roost (upper line), or more than two hours after the arrival at the roost (lower line); same data as in Fig. 1.

weight loss was high and decreased after three or four hours of roosting. In order to plot the actual course of weight loss during the roosting period, we calculated the weight loss separately for all possible combinations of the two times of weighing. Weighings at one and two hours after arrival estimate weight loss over the second hour after arrival. But, the weight loss between other combinations of times of catching can be calculated in two ways. First, directly, as the difference in the weights at, for example, hour 1 and hour 3, and second, indirectly, by adding the weight loss in birds weighed at hours 2 and 3 to the weight loss in birds weighed at hours 1 and 2. Both estimates were averaged, weighted for the number of birds in each sample. The cumulative weight loss at hour 4, and successive hours after arrival, were calculated in the same way, and are shown in Fig. 3. This figure also shows the average weight decrease obtained from samples of birds weighed at different times after their arrival at the roost. The weight decrease for individual birds closely resembles the average weight decrease in the popu-

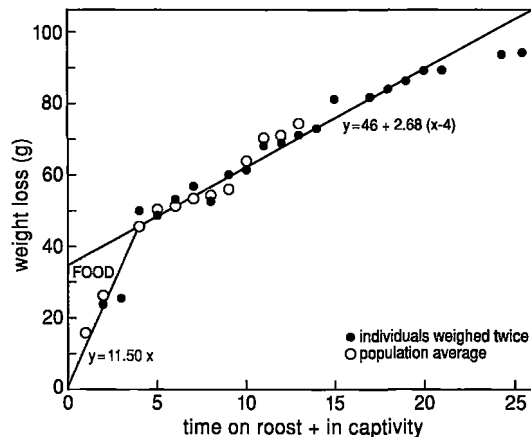


Fig. 3. Cumulative loss of body weight (g) following arrival at the roost in individuals weighed twice or calculated from the population averages.

lation. Oystercatchers lose 11.5 g h^{-1} , on average, during their first four hours at the roost, equivalent to 2-2.3% of their body weight per hour. The weight decrease from hour 4 onwards was 2.68 g h^{-1} , on average, or 0.5% of the body weight. The weight decrease on the roost was investigated separately per day and per season, but no differences were found.

The total weight loss during the first day in 314 birds held in captivity amounted to 100 g. Of this, 35 g can be attributed to excretion of stored food so that 65 g must be due to an actual loss of body weight (Fig. 3). The weight loss in fifty birds kept in captivity for two days was 137 g. Thus weight loss during the second day was much lower, being $137 - 100$, or 37 g, or 1.54 g h^{-1} , on average. However, it is not likely that the birds stored for two days also lost 100 g during the first day, since all had leg cramp right from the beginning and were inactive during captivity. This was in contrast to birds released within 24 hours after capture, which walked around in their cage restlessly.

The water content of birds decreased during captivity at a rate of 1.82 g h^{-1} ($\text{SE} = 0.30$; Fig. 4A), this representing the difference between total water turn-over minus metabolically produced

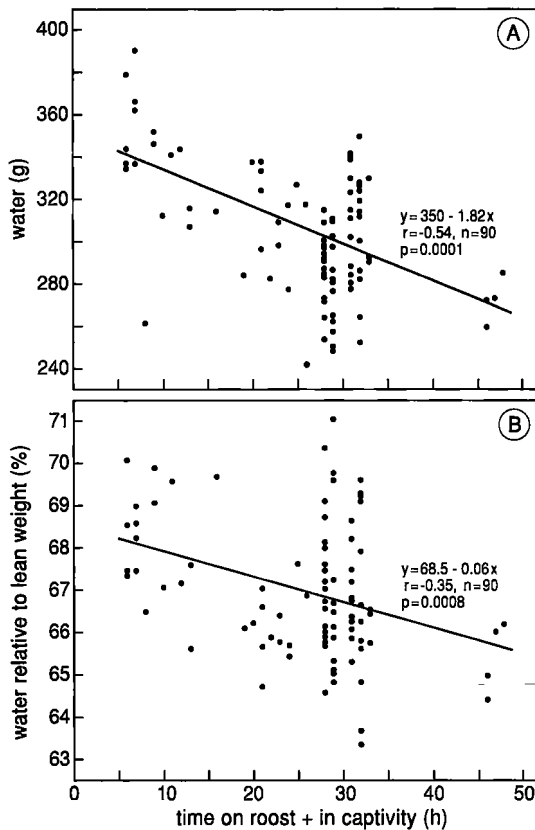


Fig. 4. (A) Absolute (g) or (B) relative (%) weight of body water in Oystercatchers as a function of the time since arrival at the roost. Relative weight of the body water is expressed as percent of the fat-free body weight. If wing length (W , mm) is included in a multiple regression analysis, the effect of time since arrival at the roost (R , hour) on the content of body water (B , g) appeared to be slightly smaller than in the simple regression: $B = 47 + 1.16W - 1.75R$ ($R^2 = 0.56$; $p = 0.03$ for wing and $p < 0.0001$ for roosting time). The effect of R on the relative amount of body water ($BW\%$) is larger after inclusion of wing length: $BW\% = 80 - 0.04W - 0.07R$ ($R^2 = 0.44$; $p = 0.15$ for wing and $p < 0.001$ for roosting time).

water. The large variation around the regression is due to differences in body size. If wing length - as a measure of body size - is also included in a multiple regression analysis, the net water loss appeared to be slightly smaller at 1.75 g h^{-1} ($SE =$

0.37), or 42 g day^{-1} . The decline in the water content may be due to dehydration or to loss of lean body weight. If there were no dehydration, the water content relative to the fat-free dry mass would remain at the same level. The relative water content decreased significantly, however, at a rate of $0.059\% \text{ h}^{-1}$ ($SE = 0.017$). This represents a decrease from 68.5% at the time of their arrival at the high water roost to 67% after 24 hours (Fig. 4B). The estimated relative water loss is even larger, $0.071\% \text{ h}^{-1}$ ($SE = 0.020$) when wing length was taken into account in a multiple regression analysis. From this we conclude that, from the estimated water loss of 42 g day^{-1} , $350 \text{ g water} \times 0.071\% \times 24 \text{ h} = 6 \text{ g}$ may be attributed to dehydration and thus 36 g to the loss of water from the flesh.

There was, in the same sample of birds, no significant decrease in the fat weight, neither absolutely, nor as proportion of total body weight. Fat loss was not measurable since the birds were collected on different dates and the variation in fat weight between days was much larger than the variation within days, and the data set was too small to analyse the fat loss against date.

DISCUSSION

Weight loss and defecation

The initial high weight loss is due to the emptying of the digestive tract. Other studies (Lloyd *et al.* 1979, Wilson & Davidson 1982, Davidson 1983, Goede & Nieboer 1983, Schick 1983, Zwarts *et al.* 1990) have also found in waders a higher rate of weight loss in the first one or two hours after capture than subsequently. In most of these studies, waders were caught shortly after their arrival at the roost. No decrease in the rate of weight loss after capture was found, however, by OAG Münster (1975, 1976, 1983) in waders captured at a nocturnal roost in a non-tidal area. Perhaps these birds had already emptied their alimentary tract before they were weighed. Apart from this one case, an especially high rate of weight loss at the start of the roosting period seems to be general.

Kersten & Visser (1996a) found that captive Oystercatchers while feeding on mussel flesh lose continuously 0.16 g min^{-1} due to defecation and 0.07 g min^{-1} as water from the nasal glands. This is equivalent to a combined loss of 13.8 g h^{-1} , so slightly higher than the weight loss of 11.5 g h^{-1} recorded by us during the first four hours at the roost. However, the value of 11.5 g h^{-1} is an average. If some individuals arrive at the roost with almost emptied guts, their rate of weight decrease would be close to the loss of 2.68 g h^{-1} observed in birds which have defecated all their food (Fig. 3). Consequently, the frequency distribution of the weight loss in the individuals in the first four hours after arrival would be skewed to the left, with the majority of the individuals falling just above the calculated average of 11.5 g h^{-1} . This probably explains why the initial average weight loss at the roost is lower than measured by Kersten & Visser (1996a) in Oystercatchers with food in their stomachs.

Kersten & Visser (1996a) showed that it takes an Oystercatcher five hours to digest the 85 gram of bivalve flesh, the maximum found in the guts of birds flying to the roost by Dare & Mercer (1973). This is a maximum. Drinnan (1958) found that Oystercatchers leaving the feeding area usually contained 50 to 70 g of food. Figure 3 suggests that the average Oystercatcher arriving at the high water roost has stored 35 g of food, thus filling up less than half of their digestive tract. But Fig. 3 shows the weight loss relative to the time of arrival at the roost whereas, in fact, the birds usually stop feeding some time before. Our observations show that they stop feeding when the incoming tide reaches the level of 0 cm relative to mean sea level (Zwarts *et al.* 1996b), which is, on average, one hour before it reaches +20 cm and the birds fly to the roost. Although it has no consequence for the interpretation of the weight loss of Oystercatchers at the high water roost (Fig. 3), it may thus be noted that Oystercatchers end their feeding period, on average, not with 35 g but probably with about 47 g of stored food. However, this may still be an underestimate, because birds defecate more than usual when they are

caught and handled and so will have lost extra faeces before they are weighed. As the faeces of an Oystercatcher weigh up to 8 g (Kersten & Visser 1996a), this unmeasured loss could be quite high. In conclusion, our data do not deviate from those of Drinnan (1958), Dare & Mercer (1973) and Kersten & Visser (1996a): Oystercatchers leaving the tidal areas have stored 50-85 g fresh food.

How to correct for weight loss?

It is common practice to correct body weight relative to the time after capture. This is convenient if birds are always captured at the same time after their arrival at the roost. However, this paper has shown that this correction factor cannot be used if the time of capture varies. For instance, if birds are captured during the flight between feeding area and roost, the guts will be full on the advancing tide but empty on the receding tide. As a consequence, the rate of weight loss after capture during the flood will be 4.3 times higher than during the ebb (Fig. 3). The main reason why weight correction is usually based upon the time relative to capture, is that time of capture is usually known exactly, whereas the time at which birds stop feeding is often uncertain. However, the time at which the birds leave the feeding grounds may be estimated using a tide-table or, if possible, the continuous water level measurements of a nearby tide-gauge.

We suggest the two lines in Fig. 3 are used to correct for the weight loss at the roost: 11.5 g should be subtracted for each hour the Oystercatcher is weighed before hour 4 after their arrival at the roost and 2.68 g must be added to the weight for each hour the bird is weighed after hour 4.

Allometry of weight loss

Oystercatchers lose 2.68 g h^{-1} or 0.5% of their body weight if their guts are empty (Fig. 3). This is relatively low compared to the percentage weight loss measured in other waders with empty guts (OAG Münster 1975, 1976, 1983, Lloyd 1979, Goede & Nieboer 1983, Schick 1983, Davidson 1983, Ruiz *et al.* 1989). Zwarts *et al.* (1990) con-

cluded that the different rates of relative weight loss in different wader species are related to body size. The loss of body weight is 1% per hour for a small species, such as the Little Stint *Calidris minuta* (22 g), but 0.6% for the much larger Bar-tailed Godwit *Limosa lapponica* (253 g). The relationship found between loss of body weight (% h⁻¹) and body weight (*W*, g) for seven species was:

$$\text{weight loss h}^{-1} (\%) = 0.17 \ln(W).$$

This is equivalent to

$$\text{weight loss h}^{-1} (g) = 0.022W^{0.75}.$$

When extrapolated to the Oystercatcher (*W* = 520 g), the predicted weight loss is 2.62 g h⁻¹, very close to the rate of 2.68 we found. If the data from all available wader studies are combined (Fig. 5), weight loss is described with an allometric function, with the exponent of 0.81 (*SE* = 0.04):

$$\text{weight loss h}^{-1} (g) = 0.018W^{0.81}.$$

This is slightly higher than the value calculated for the smaller sample of data, but still does not differ from the expected exponent of 3/4.

Components of weight loss

What are the possible sources of weight loss and how can we predict them? The total net water loss in captive Oystercatchers was estimated to be 42 g day⁻¹, of which 6 g day⁻¹ was due to dehydration and 42 - 6, or 36 g day⁻¹ to water loss from catabolisation of muscles. This information can now be used to estimate the other possible components of weight loss in birds after all the food has been defecated. If the water content of muscles is known, the weight loss of the dry flesh itself can be derived. The water content of lean body tissue is 68.5% (the intercept in Fig. 3B), but this figure cannot be used to estimate the dry weight of muscles because the lean body weight is defined as total dry body weight minus fat, and so also includes the feathers and skeleton. In the

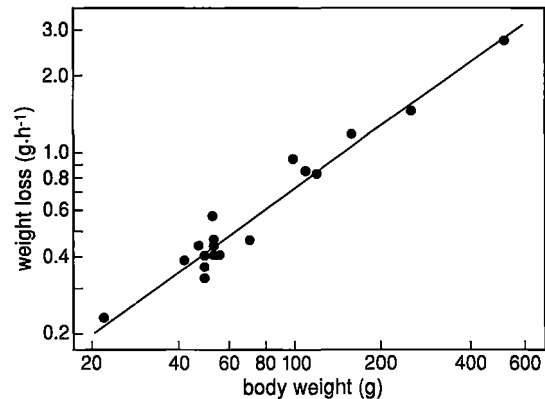


Fig. 5. Weight loss as a function of body weight in different wader species. Sources: Little Stint (Zwarts *et al.* 1990), Dunlin (OAG Münster 1976, Lloyd *et al.* 1979, Goede & Nieboer 1983, Davidson 1983, Ruiz *et al.* 1989 and Zwarts *et al.* 1990), Sanderling *Calidris alba* (Schick 1983, Zwarts *et al.* 1990), Curlew Sandpiper *Calidris ferruginea* (OAG Münster 1983, Zwarts *et al.* 1990), Turnstone *Arenaria interpres* (Zwarts *et al.* 1990), Knot (Davidson 1983, Zwarts *et al.* 1990), Common Snipe *Gallinago gallinago* (OAG Münster 1975), Bar-tailed Godwit (Zwarts *et al.* 1990) and Oystercatcher (this study). *R*² = 0.95.

Oystercatcher, the dry weight of the feathers amounts to 30 g (Kersten & Piersma 1987), whereas the dry skeleton weighs 31 g (Prange *et al.* 1979, Graveland *et al.* 1995). Hence the water content is 79.7% of the fat-free flesh weight of 421 g, a value obtained by subtracting the weight of feathers (30 g) and skeleton (31 g) from the total fat-free body weight of 500 g (Zwarts *et al.* 1996a). Assuming that the water content of the Oystercatcher flesh is indeed 80%, we can estimate that, if water loss by catabolisation of muscles is 36 g, the estimated loss of lean dry flesh must be 9.2 g day⁻¹. The total loss of body weight is 64 g day⁻¹, so some weight loss is still unexplained: 64 g - (6 g due to dehydration + 36 g due to water loss from catabolisation + 9.2 g dry flesh), or 12.8 g day⁻¹. We assume that this must be due to metabolism of fat. This means that 58% of the decrease in dry body weight would be due to loss of fat and 42% of nonfat. These estimates

are approximate, but do not deviate much from the measurements of Davidson (1983), who found that 50% and 45% of the dry weight loss consisted of fat in Dunlin *Calidris alpina* and Knot *Calidris canutus*, respectively. These values are low, however, compared to the 80% fat deposited as winter reserve by Oystercatchers in late autumn (Zwarts *et al.* 1996a). We found no seasonal variation in the weight loss. This suggests that also the relative amounts of fat and protein being catabolized does not change during the course of the year, despite the large variation in the amount of fat being deposited (Zwarts *et al.* 1996a).

The estimated loss of fat and lean weight allows the energy consequences of stress induced by captivity to be estimated. The energy density of fat is 38.9 kJ and for dry protein 22.6 kJ (Whitow 1986). The energy catabolized during starvation can now be estimated to be 700 kJ day⁻¹, of which dry protein delivers 9.2 g day⁻¹ × 22.6 kJ g⁻¹ = 200 kJ day⁻¹ and fat 12.8 g day⁻¹ × 38.9 kJ g⁻¹ = 500 kJ day⁻¹. The basal metabolic rate of an Oystercatcher is 250 kJ day⁻¹ (Kersten & Piersma 1987). The normal cost of living of a captive Oystercatcher in thermoneutral conditions is 600 kJ day⁻¹, this being equivalent to 2.4 times the basal metabolic rate (Kersten & Piersma 1987). In contrast, the observed weight loss and estimated change in body composition in our captive birds suggests that energy metabolism occurs at the slightly higher rate of 2.8 times the basal metabolic rate. This is of course an estimate based on several extrapolations and assumptions, but a higher rate of energy expenditure is to be expected in stressed, and restless captive, birds. For instance, the heart rates of Oystercatchers is twice as high as normal when they are handled, even though they appear calm (Speakman 1984).

Oystercatchers held for years in captivity lose 30 g of their body weight during a day when they took no food (Kersten & Piersma 1987). A similar value was found in free-living Oystercatchers breeding their eggs (Kersten & Visser 1996b). The much higher weight loss found by us in birds during the first day after capture (64 instead of 30 g day⁻¹) is only partly due to presumed dehydration

(6 g day⁻¹) and higher energy demands (9 g day⁻¹). Most important is probably the presumed low fat fraction. At a loss of 30 g of their body weight during a day, the energy density of the catabolized tissue must have been 600/30, or 20 kJ g⁻¹ wet weight, which is 1.7 times the estimated value of 12 kJ in the birds after capture, given that the loss of body weight, exclusive dehydration, was 58 g and equivalent to 700 kJ. It is unknown to what degree the lower weight loss in birds with leg cramp kept in captivity for two days is due to their inactivity, and thus lower metabolism, or to a higher energy density of the catabolized tissue.

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SAMENVATTING

Het verteringskanaal van een Scholekster kan 0 maar ook 85 g voedsel bevatten. In het laatste geval gaat het om zo'n 16% van het lichaamsgewicht. Om voor deze variatie te corrigeren, is het gebruikelijk om de gewichten veelal te standaardiseren naar een bepaalde tijd na de vangst. Dit artikel laat zien dat het veel beter is te corrigeren naar het tijdstip waarop de vogels gestopt zijn met voedselzoeken. Tijdens het verteren van het voedsel verliest de vogel 11.5 g per uur. Gemiddeld gaat dat door tot vier uur na het verlaten van het voedselgebied. Daarna verliest de Scholekster 2.68 g per uur, of 0.5% ten opzichte van het lichaamsgewicht (Fig. 3). Op dagbasis betekent dit een verlies van 68 g per dag. Voor een klein deel is dit te verklaren met uitdroging (Fig. 4). Het verlies blijft erg groot in vergelijking met een wilde Scholekster omdat die na een dag zonder eten slechts 30 g verliest. Pas gevangen wilde Scholeksters zijn zeer onrustig en geven daardoor waarschijnlijk extra energie uit. Bovendien verbranden ze relatief veel eiwit en weinig vet. Dit is wellicht ook zo bij andere steltlopers kort na gevangenschap, want het % gewichtsverlies bij de Scholekster is niet anders dan bij andere steltloper-soorten. Kleinere steltloper-soorten verliezen 1% lichaamsgewicht per uur en dat neemt af bij de zwaardere soorten tot 0.5% (Fig. 5).